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The Heliotropic Responses Of Avena Sativa

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THE HELIOTROPIC RESPONSES OF AVENA SATIVA

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The Heliotropic Responses of Avena sativa.

All plants orient themselves in response to external stimuli such as those produced by gravity, light, heat, and moisture. Light is one of the most important of these factors. The response to unilateral light is known as heliotropism or phototropism. When the curvature of a plant or organ is toward the source of light it is positive, when away from the source, negative. Different plants are attuned to varying degrees of intensity so that light sufficient to cause a ready response in one plant in many instances is without apparent effect upon other plants.

A plant does not generally respond immediately upon receiving a stimulus. The lapse of time from the moment it is subjected to a stimulus until the time when the response to that stimulus becomes visible is known as the reaction period. The shortest period during which a plant can receive a stimulus to which it will react is the presentation or induction period. This is, of course, the first part of the reaction period. The remainder of the reaction period is the latent period and is the time after full perception until the manifestation of the response to the stimulus.

The presentation, latent, and reaction periods vary for different kinds of plants and in the same plant under different external conditions or maturity. Gravity is a constant factor.

The negative geotropism of shoots or the stimulus which causes them to grow away from the center of gravity acts in oppostion to the heliotropic stimulus which induces plants to turn at some angle from the vertical. It is this negative geotropism that causes seedlings placed horizontally to turn upward and those that have turned toward light to straighten again when left in the dark. Since the force exerted by gravity does not change in these experiments it will not be further considered. Others of these external conditions do change and must be controlled in careful experimentation. Some of the varying factors with which we must deal are heat, moisture, the physical and chemical properties of the light, the air in which the experiments are preformed and the "tonus" of the plants in question.

In 1878 Wiesner studied the effect of the intensity and wave lenght of light upon heliotropic response. He found that the violet end of the spectrum produced curvature the most readily, that the yellow rays exerted no influence, and that the red rays again induced a response. By placing plants at measured distances from a known constant source of light he determined the effect of intensity upon the time of response and upon the angle of curvature. Thus he found that Vicia sativa with a light of .5 "Walrathkerze" intensity turned 90° in 1 hour 10 minutes. If the intensity was greater or less than this the reaction was not so rapid. Later (1893 p.348) Wiesner determined that Vicia sativa

was still sensitive to a light with a chemical intensity of .00000016 Roscoe-Bunsen units. In 1895 he experimented further with the chemical intensity of light but since he studied the formation of organs rather than their tropic responses these results do not apply here directly.

Figdor, a pupil of Wiesner, also studied the effect of light upon seedlings. He determined the lowest intensities to which various plants responded. Thus ('93 p.50-54) Vicia sativa reacted to .0025574 Normalkerzen, Helianthus annuus to .003996 and Lepidium sativum to .0003262 Normalkerzen.

Oltmanns ('97 p.4) showed that plants could react in three ways to light. At a certain intensity light caused a negative curvature, at another no response, and at a less intensity a positive curvature. For example where the intensity of the electric arc was equal to 8000 Hefner lamps, or 80 centimeters from the light Phycomyces responded positively, where, however the intensity was 100,000 Hefner lamps, or 20 to 30 centimeters from the light, the sporangiophores responded negatively. At a distance of 60 to 70 centimeters from the light the plants were indifferent.

Fröschel, experimenting with Lepidium sativum, saw a relation between intensity and response that previous investigators had overlooked. He summed up his results by stating ('07 p.255) that the presentation period decreased as the intensity

increased or that the product of the intensity of the light and the length of the presentation period was constant. He also found that Lepidium sativum had a presentation period as short as 2 seconds with the proper light intensity.

The results of Wiesner and Figdor briefly stated above need verification because the men neglected entirely a factor which later investigators have shown to be of great importance. They used luminous gas flames as sources of light. From such a flame there escape unburned gases and products of combustion. Such gases influence the response of plants to light as proved by Molisch and Richter. Molisch (1905 p.8) asserted that traces of illuminating gas found in the air of the laboratory were sufficient to so modify the sensitiveness of a plant that it responded to light produced by phosphorescent bacteria and by radium in impure air when it would not under the same conditions respond in pure air. Ervum lens and Vicia sativa seedlings behaved in this manner. Richter (1906 p.330) proved that seedlings reacted differently to the same intensity of light if all factors, excepting the composition of the air, were the same in both cases. The response in pure air was entirely wanting at the same intensity at which it had become very apparent in impure air. If the intensity was increased sufficiently the plants also responded in the pure air but, with the same intensity and plants of the same age, the angle of curvature was greater

in the impure than in the pure air. The seedlings with which he experimented were varieties of Vicia, Vicia sativa being the most sensitive to its environment.

Another factor commonly neglected is heat. Czapek and Bach considered the effect of temperature upon responses. Altho they experimented principally with geotropism, the same factors doubtless influence other tropic responses. Czapek (1898 p. 197) obtained results that may be summed up in the following table.

Temperature	0°	5°	10°	15°	20°	25°	30°	39°
Presentation period	18hr	45min	30	20	20	20	20	25
Reaction period	∞	360	120	80	80	80	70	120

These experiments were performed with the roots of Lupinus albus. From these and previous observations he drew the conclusion that the presentation period was little affected by heat, excepting extremely low and high temperatures. The relative independence of temperature differences ranging from 15° to 35°C he thought characteristic of geotropic responses (1898 p. 198).

Bach, controlling outside factors better than Czapek, found that temperatures ranging from 14° to 30°C caused a great variation in the presentation period. He obtained (1907 p. 69) the following results for Vicia faba seedlings.

Temperature	14°	17°	20°	25°	30°	35°
Presentation period	14min.	11min.	7½min	3min	2min.	4min.

It is these temperatures between 14° and 30°C that effect laboratory work and according to Bach they certainly influence the presentation period, causing it to be 7 times as long at 14° as at 30°. He also found (1907 p.75) that if seedlings were kept at a temperature of 4°-10°C and then brought into optimum or room temperature, the first low temperature exerted a retarding effect upon the presentation and reaction periods.

Oltmanns and more recently Pringsheim have determined the effect of the "tonus" or "Stimmung" of seedlings to consequent response. Oltmanns (1892 p. 220) (1897 p. 6) found that when Phycomyces was constantly exposed to light it changed its sensitiveness to this light. Sporangiophores which were negative at the beginning of the experiment later became indifferent or even reacted positively. Etiolated seedlings (1897 p.14) of barley and cress did not react as rapidly to sunlight as seedlings that had been grown in the sunlight and were attuned to this intensity of light. The results obtained by Pringsheim are mentioned with more detail later.

Most of the above experiments are lacking in that the investigators did not sufficiently control all the factors that influence heliotropic response. Wiesner and Figdor had light of known intensity and their methods of experimentation were definite and exact but heat and gases in the laboratory due to the unprotected gas flames used probably affected their results. Czapek

and Pringsheim gave us no definite data on the intensity of the lights used and so their results cannot be well compared with later work. In order that heliotropic experiments may be of the greatest value all factors that influence results must be taken into consideration.

The criticism of H. Fitting in "Die Botanische Zeitung" Oct.1908 of two recent articles on heliotropism led me to undertake the following experiments. Fröschel's determination of a very short presentation period and of the intimate relation between the presentation period and the intensity of light showed that by more careful experimentation results of value can be obtained. Pringsheim neglected many of the factors that influence responses. The effect of "Stimmung," however, was suggestive. Many of his results disagreed with our conceptions of heliotropic responses and needed to be verified. It is to this "Stimmung" that chief attention has been given.

Method and Experiments.

Avena sativa seedlings were used in all of the following experiments. The seeds were placed between moist filter papers in granite iron pans where it took about 48 hours for them to germinate. The germinated seeds with roots 1/2 to 1 centimeter long were planted, about 15 in a row, in pots of moist sand. The pots were placed in a bed of damp sand and covered with common clay flower pots. These were pressed down into the sand to exclude light. Tin cans were turned over the flower pots, effectively shutting out light from above. In 48 to 52 hours the plants were generally large enough to use, being 1 to 2.5 centimeters tall. The plants were grown in the greenhouse where no gas was burned, the ventilation was good, and consequently the air quite pure. The temperature here, however, was a source of constant trouble since it could not be kept constant. Often during the night it sank to 12°C and rose in the afternoon to 30°C.

The seedlings were subjected to artificial light in a dark room. Since this room was heated only during the day, the seedlings could not be grown here as would have been preferable. The temperatures in this room ranged from 18° to 25°C for for different experiments but never changed more than 1° for a single experiment. No experiments were undertaken when the temperature was below 18° or above 25°C. The room was well venti-

lated, heated by steam, and lighted by electric lights so that the air was free of those impurities generally found in laboratories.

An 8 candle power electric light was used as a source of light. By means of a photometer and a Hefner lamp the intensity of this light was determined. From this was computed the intensity of the light at the various distances from the source at which the plants were exposed. At 1 meter this intensity was 12.6 Hefner lamps, (H.1) at 2 meters it was 3.5 H.1., at 3 meters 1.4 H.1., at 4 meters .8 H.1., and at 5 meters .5 H.1. Arcs 1, 2, 3, 4, and 5 meters from the source of light were drawn upon the table and upon these lines the pots were placed. The pots 5 meters from the light were exposed first so that these plants would not be shaded by pots nearer the light.

The first experiments were undertaken to determine the presentation period of Avena sativa. To obtain this the covers were lifted from the pots hitherto kept in the dark, the plants exposed to light the desired length of time, and the covers replaced. The shortest length of time necessary to expose seedlings so that they show a response is the presentation period. While the plants were exposed to the light all crooked seedlings were removed. After all the plants were exposed, the light was turned off. The plants were not examined until the end of the reaction period (45-60 min.) so that they might not respond to intermittant stimuli produced by exposing them to light several

times. Since the temperature at which the plants were grown and at which they were subjected to light influenced the response, the results obtained in different series are not always uniform.

The following table is a summary of a number of experiments that were performed to determine the presentation period. This shows that at a distance of 5 meters Avena sativa will respond if exposed to light for 1 minute, at 4 meters if exposed only 30 seconds, at 3 meters if exposed 15 seconds, at 2 meters if exposed 15 seconds, at 1 meter if exposed 10 seconds and at 1/4 meter if exposed 2 seconds. Shorter periods have not been studied.

Table 1.

Temp. 20-23.

No	Distance from light	Time exposed	Total no	No. reacting
1	6 meters	5 minutes	5	4
2	5 "	5 "	3	3
3	5 "	3 "	8	8
4	5 "	2 "	14	10
5	5 "	1 "	13	8
6	4 "	6 "	5	5
7	4 "	5 "	7	7
8	4 "	4 "	5	5
9	4 "	3 "	9	8
10	4 "	2 "	13	10

No	Distance from light	Time exposed	Total no	No. reacting
11	4 meters	1 minute	19	9
12	4 "	1/2 "	16	12
13	3 "	5 "	5	5
14	3 "	4 "	5	5
15	3 "	3 "	6	6
16	3 "	2 "	10	9
17	3 "	1 "	15	15
18	3 "	30 seconds	12	12
19	3 "	15 "	17	13
20	2 "	4 minutes	6	6
21	2 "	3 "	4	3
22	2 "	2 "	12	11
23	2 "	1 "	14	14
24	2 "	30 seconds	24	19
25	2 "	15 "	13	13
26	1 "	3 minutes	4	4
27	1 "	2 "	4	4
28	1 "	1 "	13	11
29	1 "	30 seconds	19	19
30	1 "	20 "	20	15
31	1 "	10 "	21	18
32	.75 "	60 "	2	2
33	.75 "	30 "	6	6

No.	Distance from light	Time exposed	Total no.	No. reacting
34	.75 meters	15 seconds	22	21
35	.75 "	5 "	28	18
36	.5 "	3 minutes	6	3
37	.5 "	2 "	2	2
38	.5 "	1 "	15	15
39	.5 "	30 seconds	4	4
40	.5	15 "	6	5
41	.5 "	10 "	13	12
42	.5 "	5 "	26	20
43	.25 "	60 "	8	7
44	.25 "	30 "	6	6
45	.25 "	15 "	8	8
46	.25 "	10 "	10	8
47	.25 "	5 "	20	20
48	.25 "	2 "	8	8

Jost ('08 p.563) says that the degree of dependence of the presentation period upon the intensity of light has not been determined. Fröschel ('08 p.255) found that the presentation period decreased as the light increased, and that the product of the intensity and presentation period was constant. The following experiments show that the presentation period does depend upon the intensity, growing shorter as the light intensity increased.

Table 11 shows the results obtained when testing Fröschel's second conclusion.

Table 11.

No.	Distance from light	Seedlings	No. reacting
1	1 meter	12	8
2	2 meters	12	10
3	3 "	11	7
4	4 "	13	9
5	5 "	11	9

No.	Presentation period	Intensity	Product
1	2 seconds	12.6	25.2
2	7 "	3.5	24.5
3	15 "	1.4	22.
4	30 "	.8	24.
5	50 "	.5	25.

This single test gives results similar to those obtained by Fröschel. Before conclusive statements can be made regarding results like the above, experiments must be made with many more seedlings. Such experiments are now under way.

Table 1 and 11 also show that the presentation period is much shorter for Avena sativa than thus far determined. In ('95 p.343) Czapek gives it as 15 minutes, in ('98 p.185) as

7 minutes. At the proper intensity of light it is at least as short as 2 seconds.

The reaction period for Avena seedlings was also determined and found to vary from 30 to 75 minutes. To obtain this the plants were left uncovered and exposed to unilateral light during the entire period.

At 2m. from the source of light, at a temperature of 25°C, the following table was obtained.

Table III.

30	35	40	45	50	55	60	65	70	75
10	54	96	149	164	169	179	182	182	183

The upper line in the table represents the time of reaction; the lower the number of plants from a total of 183 that responded for each period of time. No definite relation was found between the presentation period and the reaction period or between the intensity of the light and the reaction period. Plants 5 meters from the light reacted almost as rapidly as those only 1 meter from the light. The time within which most of the seedlings react is 45 minutes altho for a small number the reaction period is as short as 30 minutes while for others it is 60 minutes or even more.

Wiesner, Figdor, Oltmanns, Strasburger, and others

have noticed that isolated seedlings reacted differently toward light than such plants as have been grown in the light. For example, Oltmanns ('97 p.10) found that by continuous illumination the "Lichtstimmung" of Phycomyces was increased or that sporangiophores that were negative at the beginning of the experiment became indifferent or even reacted positively after several hours of exposure. Pringsheim carried on quite extensive experiments regarding the effect of exposure to light for different periods. He said ('07 p.303) that the first part of the illumination of plants with a low "tonus" caused no heliotropic stimulation but served only to raise the "Stimmung" of the plants. He neglected many factors that influence response so that his results need verification. The gas lamp which he used radiated heat ('07 p.269) which may have caused his plants, especially those set up within 30cm. of the light to be influenced by heat as Bach's experiments show. The lamp also contaminated the air of his laboratory. This may have caused an error in his results. The intensity of light, a very important item, is not mentioned. The almost complete absence of tables leads one to doubt statements that disagree so radically with our previous conceptions of heliotropic responses. Pringsheim used several kinds of seedlings but gave his results as applying equally to all.

The writer has repeated some of the experiments of

Pringsheim. with Avena sativa. Pringsheim found that the reaction period for Avena was 45-50 minutes. This agrees with the results as shown by Table 111. Pringsheim found that the reaction period could be reduced to 25-30 minutes ('07 p.277) when plants grown in the light were exposed 30cm. from the "Auerstrumpf." No tables are given for Avena and no mention is made of difficulties in obtaining responses. It was found that when the plants were grown in sunlight they were poor for purposes of experimentation because the coleoptile was generally broken when it was but a short distance (7-10mm.) above the ground. The seedlings with the pierced coleoptile will not respond to light as is well known. An exposure to sunlight for periods as short as an hour was found to have the same effect upon "Stimmung" as growth in sunlight. (Pringsheim '07 p.278).

The experiments along this line give the following results.

Table 1V.

Exposure to sunlight	Dist.fr.8cp.	Total no.	30	35	40	45	50	55	60	65	70	75
6 hours	1/2 meter	12	-	-	-	-	-	2	2	2	2	2
none	1/2 "	11	-	-	-	1	3	7	8	11	11	11
21/4 hours	1/2 "	10	-	-	-	-	-	-	-	2	2	4
none	1/2 "	12	-	-	2	5	10	11	11	12	12	12
1/2 hour	1 "	10	2	3	4	6	10	10	10	10	10	10
none	1 "	12	1	1	3	6	12	12	12	12	12	12

The above table shows that the response to artificial light is no more rapid for plants exposed to sunlight than for etiolated seedlings. Plants rotated on the klinostat for 1/2 hour in sunlight and then exposed to unilateral sunlight at the same time that seedlings hitherto kept in the dark were exposed, showed a shortening of the reaction period in favor of those rotated in the sunlight. This shows that it is a difference of intensity that causes the variation in results for sunlight and the electric lamp.

Pringsheim tested the effect of short illumination upon response in two ways, (1) by rotating the plants on a klinostat before exposing them to unilateral light, and (2) by turning them 180° after a period of unilateral illumination.

The plants for the first method were rotated "in der Nähe der Auerlampe" (intensity not given), where the reaction period was 60 minutes. One set of plants was rotated on the klinostat 5, 10, 30 minutes, then the rotation was stopped and the plants exposed to unilateral light. When the klinostats were stopped, there were placed besides the plants rotated, checks that had been in the dark up to this time. Thus the period of unilateral illumination was the same for both sets of plants.

[1]8 of 12 broke coleoptile.
[2]6 of 10 " "

The results of the above methods of experimentation Pringsheim ('07 p.279) reports as follows: "...zwar wurde die Reaktionszeit unter diesen Umständen um genau so viel verkürzt, wie die Dauer der Vorbelichtung betragen hatte. Wurde also 15 Minuten vorbelichtet so reagierten die Keimlinge in 45 Minuten, während die Vergleichspflanzen 60 Minuten brauchten, wurde 10 Minuten vorbelichtet so betrug die Reaktionszeit 50 Minuten u.s.f."

The table that follows gives the results obtained by repeating Pringsheim's experiments.

Table V.

Rotated on klinostat	Dist.fr.8cp.	Total no.	30	40	50	60	70	80	90
5 minutes	1 meter	17	5	16	17				
--------	1 "	11	8	10	11				
10 minutes	1 "	16	-	5	11	11			
--------	1 "	7	-	2	4	5			
30 minutes	2 "	60	-	-	-	6	38	56	60
--------	2 "	55	3	27	50	55			

The results do not harmonize with Pringsheim's interpretations. In the use of the klinostat in these experiments the rotation must be slow enough to prevent the development of a sufficient centrifugal force to produce a response. On the other hand the period of rotation must be sufficiently fast to prevent

a heliotropic stimulus during the movement thru a quadrant. This is impossible. Since the presentation period is as short as 2 seconds it is apparent that the period of rotation must be more rapid than 1 revolution per 8 seconds. To increase the speed of rotation to this rate causes the seedlings to respond to centrifugal force. If, then, it rotates only once in 15 minutes, during almost 5 minutes the same side of the plant will be continuously exposed and naturally react in the direction of this first stimulus. When the plants were rotated 10 minutes a retardation in reaction was quite evident. This retardation becomes more noticeable when the plants were rotated 30 minutes. More experiments of this nature are now under way. In these both the effect of time of rotation and the intensity of the light are to be determined. Pringsheim also tested the effect of rotation by exposing both the rotating pot and the check at the same time, the check, of course, to unilateral light. He found that both pots reacted at the same time if he did not rotate longer than 25 to 30 minutes ('07 p.279). This he interpreted as proving that the reaction time was shortened from 60 to 30 or 35 minutes.

Table VI gives results obtained by the same method of experimentation. After A and B had been rotated 30 minutes they were exposed to unilateral light 2 meters from source.

Table Vl.

	Rotated on klinostat	Dist.fr.light	Total no.	30	40	50	60	70	80	90
A	30 minutes	1 meter	53	-	-	-	6	19	34	53
B	30 "	3 "	52	-	-	-	6	43	52	52
C	30 "	2 "	60	-	-	-	7	38	56	60
D	--------	2 "	56	9	37	56	56	56	56	56

This table shows that plants rotated on a klinostat the first 30 minutes of their exposure do not react as rapidly as that that had continuous unilateral exposure. It also shows that plants rotated at 2 meters from the light do not respond more rapidly than those rotated 1 or 3 meters from the light. According to Pringsheim, a different "Stimmung" should here be manifested.

Table Vll.

Rotated on klinostat	Dist.fr.light	Total no.	30	40	50	60	70	80	90
30 minutes	1 meter	104	-	-	1	11	53	91	102
30 "	3 "	98	-	-	11	29	71	91	98
30 "	2 "	99	-	-	8	26	74	96	99
---------	2 "	102	2	44	83	98	101	102	102

In the experiments recorded in Table Vll the light was suspended above the plants on the klinostats. Since the tips

and flanks of the seedlings may not be equally sensitive these results in themselves are not conclusive.

Since Pringsheim was by his first experiments led to believe that the seedlings were indifferent to the direction of illumination during the first part of the reaction period, he tested his theory in another way. He exposed the plants to unilateral light for various lengths of time (the maximum being 25 minutes), turned them 180°, and continued the exposure. He gives no tables but makes this statement ('07 p.279), "Auch diese Umkehrung wirkte nicht verzögernd auf die Reaktion ein. Es ergab sich also das scheinbar so merkwürdige Resultat, dass eine Beleuchtung von der Hinterseite eine Verkürzung der Reaktionszeit bewirkte."

The writer carried on a series of experiments in the same manner and obtained contrary results. These are summarized in the following table.

Table VIII.

No	Exposed	Turned	Total no	40	45	50	60	70	80	90	100	110	120
1		not	41	+8	24	36	41						
2	5min.	180°	45	+5	21	36	43	45					
3	10 "	"	40		+8	22	31	39	40				
4	15 "	"	38		+1 -6	+3 -7	+14 -6	+33	38				
5	20 "	"	38		-19	-29	-25	+10 -9	+23	27	35	38	
6	25 "	"	39		-11	-20	-23	+5 -16	+16 -9	+23	33	37	39
7	30 "	"	42		-26	-36	-40	-41	-41	-21	+19	+27	36

These results conclusively show that the reaction period has been lengthened rather than shortened as Pringsheim maintained. For example by far the majority of the plants not turned (checks) reacted in 50 minutes. The majority of the plants turned 180° after 15 minutes exposure showed no positive response until after 70 minutes. Another fact to be noted is that seedlings exposed 15 minutes or longer often react positively toward the direction of the first illumination, i.e, or negatively toward the direction of the second illumination. The "Richtung der Beleuchtung" during the first part of the reaction period is thus shown to be of significance.

Consequently, revision is necessary of the statements by Pringsheim "dass nämlich der erste Teil der verlängerten Reaktionszeit bei starken Licht nur der Erhöhung der Stimmung

dient, and dass während dieser Zeit die Richtung, der Beleuchtung ohne Bedeutung ist," ('07 p.279) and "wir können demnach die verlängerte (scheinbare) Reaktionszeit in folgende Phasen auflösen! Ein Keimling mit niedriger Stimmung wird hell beleuchtet. Es findet keine tropistische Reizung statt, die Pflanze ist heliotropish indifferent. Aber das Licht ist nicht ohne Wirkung, die Stimmung steigt." ('07 p.280). The experiments on the presentation period (Table I and II) show that plants do respond heliotropically during the first 5 to 30 minutes of illumination. In fact the experiments above recorded show that they responded in a very much shorter time. Tables VI, VII, VIII show that the reaction period is not shortened by artificial illumination either by rotating the plants before the source of light or by turning them 180° after a short period of illumination.

Conclusions.

From the work completed at the present time the following conclusions may be drawn.

(1). The presentation period of Avena sativa is as short as 2 seconds, much shorter than has been found up to the present time.

(2). The presentation period increases as the intensity of light decreases.

(3). The reaction period varies from 30 to 60 minutes, most plants responding in 45 minutes in temperatures varying from 18°-25°C.

(4). Avena sativa responds heliotropically during the first 5 to 25 minutes of exposure. This period is not used entirely in raising the "Stimmung" of the plants in question.

(5). If seedlings of Avena are rotated upon a klinostat for 10 minutes or longer, 1 to 3 meters from an 8cp. electric light the reaction period is lengthened, not shortened.

(6). If plants 1 meter from an 8cp. electric light are turned 180° after an illumination of 10 to 30 minutes the reaction period is lengthened. If plants are exposed for 20 minutes before turning them 180° they will respond in the direction of first illumination before they respond in the direction of

second illumination.

(7). An illumination of 30 minutes to the artificial light used shows no appreciable effect upon the "Stimmung" of Avena sativa.

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